

3. Review of the Higher Classification of the Lepidoptera, with Special Reference to Lower Heteroneurans

Ebbe Schmidt NIELSEN

Zoological Museum, Copenhagen, Denmark

Present address: Division of Entomology, CSIRO, P.O. Box 1700,
Canberra City, A.C.T. 2601, Australia

Our knowledge of the phylogeny (on the suborder level) of the Lepidoptera has increased markedly during the last four decades, primarily because of increasing studies of the morphology and diversity of the primitive (non-ditrysian) Lepidoptera and because of the availability of a well-reasoned methodology (HENNIG, 1966) for phylogenetic analysis.

The first phylogenetic classification of the Lepidoptera proposed by HENNIG (1953 – mainly based on HINTON's (1946) observations) has since proved basically correct and has been further substantiated by several authors (see discussion and further references in COMMON (1975), DAVIS (1978) and KRISTENSEN & NIELSEN (1980, 1981)).

The presently recognized phylogeny of the lowest Lepidoptera is presented in Fig. 1, and the phylogeny of the Heteroneura is illustrated in Fig. 2.

The sister-group of the LEPIDOPTERA. The orders Lepidoptera and Trichoptera constitute the Amphiesmenoptera, the monophyly of which is generally accepted and considered among the best documented within the Insecta (HENNIG, 1969; KRISTENSEN, 1975).

Monophyly of the LEPIDOPTERA. The monophyly of the Lepidoptera (including the Zeugloptera) is well documented by a suite of autapomorphies, some of which are: (1) absence of a median ocellus, (2) presence of a pit containing sensilla on apical segment of labial palp, (3) presence of median posterior process on corporotentorium, (4) presence of protibial epiphysis and (5) presence of scale cover on wings (see discussion in KRISTENSEN, 1975).

Phylogeny of the LEPIDOPTERA. Most authors have favoured the hypothesis that the primary dichotomy in the Lepidoptera lies between Zeugloptera and all remaining Lepidoptera. However, ongoing anatomical studies on Agathiphagidae (by Dr. N. P. KRISTENSEN, Copenhagen) provide evidence that the primary dichotomy might alternatively lie between Aglossata and Zeugloptera+Glossata, and the possibility that it lies between Zeugloptera+Aglossata and Glossata cannot be entirely ruled out (KRISTENSEN & NIELSEN, 1979).

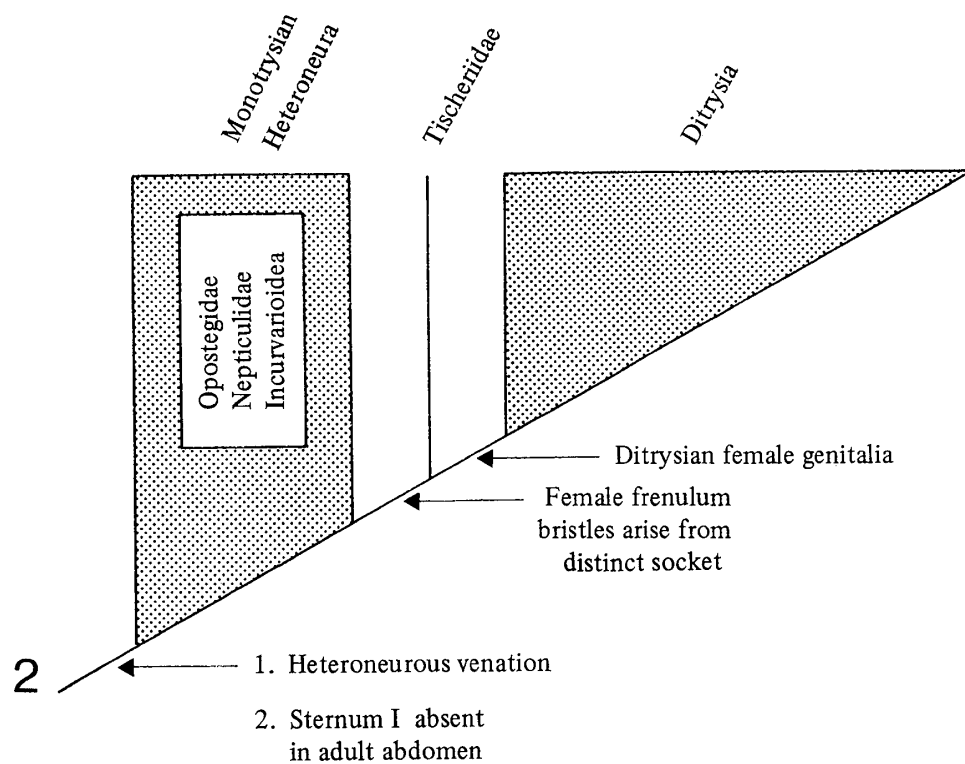
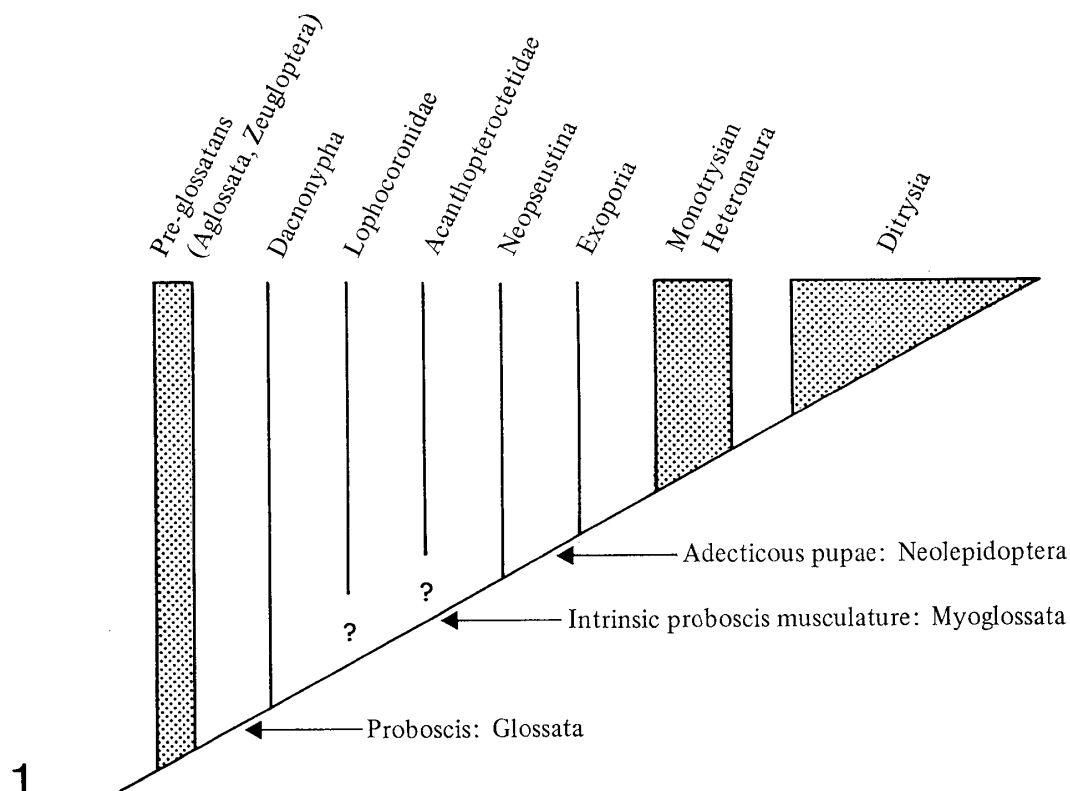
The non-glossatan grade. This grade comprises the Aglossata, with only a single included small family, the Agathiphagidae (see COMMON, 1973), and the Zeugloptera, with the Micropterigidae as the only included family (KRISTENSEN & NIELSEN, 1979).

Monophyly and phylogeny of the GLOSSATA. The monophyly of the Glossata is well substantiated by the presence of a coilable proboscis. The primary dichotomy is generally considered to lie between the Dacnonypha and the Myoglossata.

The Dacnonypha as currently delimited comprise the exclusively Northern Hemisphere family Eriocraniidae (see DAVIS, 1978) and probably also the exclusively Australian family Lophocoronidae (see COMMON, 1973). Also the small North American family Acanthopteroctetidae is assigned to the Dacnonypha (DAVIS, 1978), but in contrast to the other two dacnonyphan families, species of the Acanthopteroctetidae have hollow wing-scales (see below) and their affinities remain uncertain.

Monophyly and phylogeny of the MYOGLOSSATA. The monophyly of the Myoglossata is demonstrated by the presence of (1) intrinsic longitudinal proboscis muscles (the eriocraniid proboscis lacks intrinsic muscles) and (2) lacunate, perforated wing-scales, i.e., "normal type" scales (KRISTENSEN & NIELSEN, 1981).

The monophyly of the Neopseustina (only included family: Neopseustidae) is demonstrated by DAVIS (1975) and DAVIS & NIELSEN (1980).



Figs. 1-2. Cladograms of the lepidopteran suborders with indications of some of the major evolutionary events; further characters are discussed in the text. Fig. 1. The lowest Lepidoptera (after KRISTENSEN & NIELSEN, 1981). Fig. 2. The Heteroneura.

Monophyly and phylogeny of the NEOLEPIDOPTERA. The monophyletic nature of the Neolepidoptera is demonstrated by the following autapomorphies: (1) adult mandibular muscles reduced, (2) adecticous pupa with dorsal abdominal spines, (3) lateral displacement of free prothoracic furcal arm, (4) abdominal nerve cord sheath with copious dorsal connective tissue and (5) coiled spermathecal canal (DUGDALE, 1974; KRISTENSEN 1978b; KRISTENSEN & NIELSEN, 1980, 1981). The primary dichotomy in the Neolepidoptera lies between the Exoporia and the Heteroneura.

The monophyly of the Exoporia and the phylogeny of the exoporian families (Mnesarchaeidae, Palaeosetidae, Neotheoridae, Anomosetidae, Prototheoridae and Hepialidae) are discussed by COMMON (1975), GIBBS (1979) and KRISTENSEN (1978a, b).

Monophyly of the HETERONEURA. The monophyly of the Heteroneura is based on (1) heteroneurous venation, (2) frenular bristles and retinaculum acting as wing-coupling apparatus and (3) adult abdominal sternum I absent.

The Heteroneura comprise the monotrysian heteroneurous grade and the Ditrysia, far the most successful lepidopteran suborder and accounting for 99% of all species of Lepidoptera. The monophyletic taxa: Opostegidae, Nepticulidae, Incurvarioidea (comprising the families Heliozelidae, Adelidae, Crinopterygidae, Incurvariidae, Cecidosidae and Prodoxidae; NIELSEN, unpublished) and Tischeriidae.

Phylogeny of the monotrysian heteroneuran grade. At present the phylogeny is unsettled and no single hypothesis on the phylogenetic interrelationships between the Opostegidae, Nepticulidae and Incurvarioidea seems better substantiated than any other. Possible synapomorphies between pairs among these family groups are for Opostegidae/Nepticulidae: (1) antennal scape with well-developed eye-cap and (2) prominent metatibial spines, and for Opostegidae/Incurvarioidea: presence of pectinifer on male valva.

The Tischeriidae may represent the sister-group of the Ditrysia: all long frenular bristles arise from a distinct socket in females of Tischeriidae and Ditrysia (NIELSEN, unpublished). This new formation seems unparalleled, but the suggested sister-group relationship needs further scrutiny.

Monophyly of the DITRYSIA. The monophyly of the Ditrysia is based on (1) presence of ditrysian endoporian female genitalia and (2) dorsal position of common oviduct (see DUGDALE, 1974; COMMON, 1975).

Acknowledgement. I wish to thank Dr. N. P. KRISTENSEN for valuable comments on a draft of the manuscript.

Literature

- COMMON, I. F. B., 1973. A new family of Dacnonypha (Lepidoptera) based on three new species from Southern Australia, with notes on the Agathiphagidae. *J. Aust. ent. Soc.*, **12**: 11–23.
- 1975. Evolution and classification of the Lepidoptera. *Ann. rev. Ent.*, **20**: 183–203.
- DAVIS, D. R., 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). *Smithson. Contr. Zool.*, **210**: i–iii, 1–45.
- 1978. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopterocetidae (Lepidoptera). *Smithson. Contr. Zool.*, **251**: i–iv, 1–131.
- & E. S. NIELSEN, 1980. Description of a new genus and two new species of Neopseustidae from South America, with discussion of phylogeny and biological observations (Lepidoptera: Neopseustoidea). *Steenstrupia*, **6**: 253–289.
- DUGDALE, J. S., 1974. Female genitalia configuration in the classification of Lepidoptera. *N. Z. J. Zool.*, **1**: 127–246.
- GIBBS, G. W., 1979. Some notes on the biology and status of the Mnesarchaeidae (Lepidoptera). *N. Z. Ent.*, **7**: 2–9.
- HENNIG, W., 1951. Kritische Bemerkungen zum phylogenetischen System der Insekten. *Beitr. Ent. (Suppl.)*, **3**: 1–85.

- 1966. Phylogenetic systematics. 263 pp. Illinois Univ. Press., Urbana.
- 1969. Die Stammesgeschichte der Insekten. 436 pp. Verlag W. Kramer, Frankfurt a.M.
- HINTON, H. E., 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. *Trans. R. ent. Soc. Lond.*, **97**: 1–37.
- KRISTENSEN, N. P., 1975. The phylogeny of hexapod “orders”. A critical review of recent accounts. *Z. Zool. Syst. Evol Forsch.*, **13**: 1–44.
- 1978a. A new hepialoid familia from South America, with remarks on the phylogeny Sf the subordo Exoporia (Lepidoptera.. *Ent. Germ.*, **4**: 272–294.
- 1978b. Observations on *Anomoses hylecoetes* (Anomosetidae), with a key to the hepialoid families (Insecta: Lepidoptera). *Steenstrupia*, **5**: 1–19.
- & NIELSEN, E. S., 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). *Steenstrupia*, **5**: 69–147.
- & ——— 1980. The ventral diaphragm of primitive (non-ditrysian) Lepidoptera. A morphological and phylogenetic stydy. *Z. Zool. Syst. EvolForsch.*, **18**: 123–146.
- & ——— 1981. Intrinsic proboscis musculature in non-ditrysian Lepidoptera—Glossata: Structure and phylogenetic significance. *In* CEDERHOLM, L. (ed.): Advanced in insect systematics and phylogeny. *Ent. scand. Suppl.*, **15**: 299–304.

The interrelationships between the basic lineages in the Lepidoptera is further analysed in KRISTENSEN, N. P. and NIELSEN. (In press). The *Heterobathmia* life history elucidated: Immature stages contradict assignment of suborder Zeugloptera (Insecta, Lepidoptera). *Z. Zol. Syst. Evol-Forsch.*